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The effects of lesions op the centrifugal fibers to the retina on visually guided behavior in the pigeon (Columba livia).

Monica Seech

THE EFFECTS OF LESIONS OF THE CENTRIFUGAL FIBERS TO THE RETINA ON VISUALLY GUIDED BEHAVIOR IN THE PIGEON (*COLUMBA LIVIA*)

by

Monica Seech

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Professor in Charge

Chairman of Department

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TABLE I. LIST OF ABBREVIATIONS USED IN THIS PAPER

AP	Area pretectalis
Cb	Cerebellum
DIV	Decussation of the fourth nerve
Fb	Forebrain
GCt	Substantia grisea centralis
ICo	Nucleus intercollicularis
Imc	Nucleus isthmi, pars magnocellularis
ION	Isthmo-optic nucleus
IOT	Isthmo-optic tract
LLd	Nucleus lemnisci lateralis, pars dorsalis (Groebbels)
MLd	Nucleus mesencephalicus lateralis, pars dorsalis
OC	Optic chiasma
OT	Optic tectum
PC	Posterior commissure
RxVM	Radix mesencephalicus nervi trigemini
SPC	Nucleus tractus septomesencephalici
TC	Tectal commissure
TIT	Tecto-isthmal tract
TSM	Tractus septomesencephalicus

ABSTRACT

The present experiment was designed to further the understanding of the centrifugal fibers to the avian retina. The centrifugal fibers, in some birds at least, originate in the isthmo-optic nucleus in the midbrain, and appear to be the efferent limb of a local feedback loop to the retina. In this loop, each quadrant of the isthmo-optic nucleus projects to the retinal quadrant from which it receives its relayed input through the optic tectum. The feedback nature of this centrifugal pathway suggests some form of regulation of information transmission; studies have indicated that the centrifugal fibers generally act to increase the sensitivity of the retina.

The suggestion is made here that the centrifugal fibers to the avian retina have a role in visual guidance. Accuracy in pecking a stimulus key was examined in 13 pigeons both before and after lesions were attempted in either the isthmo-optic tracts or the area just dorsal to each tract. It was predicted that centrifugal fiber damage would result in a reduced degree of pecking accuracy.

The results of the present experiment are difficult to interpret since isthmo-optic tract damage was usually accompanied by damage to several additional structures. Thus, the effects reported below could be due in whole or in part to the additional

damage. Also, complete bilateral centrifugal fiber damage can definitely be established for only one bird.

The analysis of pecks made around the perimeter of the stimulus key shows that the difference for the 13 birds between the number of misplaced pecks, as well as the number of trials with misplaced pecks, made pre- and postoperatively is positively correlated with total amount of centrifugal fiber damage. Further, birds with isthmo-optic tract damage show a greater impairment with regard to number of trials with the misplaced pecks than do birds without tract damage. The analysis of pecks too short to activate the stimulus key considered together with those placed around the perimeter of the stimulus key yields no significant result. No result involving groups is significant in the analysis of latencies to activation of the stimulus key.

Central, or centrifugal, influences have been shown to exist in each of the major sensory pathways to the vertebrate brain. The concept of centrifugal control means that information is modified as it travels toward the brain by the feedback which the brain itself provides. Concerning the centrifugal innervation of the vertebrate retina, there is conclusive evidence for its existence only in the bird (Ogden, 1968; Rodieck, 1973). In some birds at least, fibers arising from the isthmo-optic nucleus, located in the midbrain, terminate primarily on amacrine cells in the contralateral retina. The role that this centrifugal system plays in the visual perception of the bird has yet to be completely established. The anatomical location of the isthmo-optic nucleus, namely, at the posteromedial border of the optic tectum near such structures as the cerebellum and oculomotor nucleus, suggests a possible role in visual guidance (Craigie, 1928). The present experiment was designed to test this visual guidance hypothesis with the pigeon. Before describing this study, the structural and functional data related to the centrifugal system of the pigeon will be reviewed with particular emphasis on visual guidance. The historical development of evidence supporting the existence of centrifugal fibers to the avian retina precedes this review.

Historical Perspective

Centrifugal fibers to the avian retina were described as early as 1889. In Golgi preparations of the avian retina, Cajal (1889) observed axons which terminated in the retina but did not seem to originate there; he suggested that these fibers arose from cell bodies which lay centrally within the brain. Dogiel (1895) observed similar fibers in methylene-blue preparations of the avian retina and traced them back into the optic nerve head. The first experimental evidence for the central origin of these fibers was provided by Perlia (1889) who, some months after enucleating an eye of a newly hatched chick, observed that a distinct cell mass in the caudal midbrain was totally atrophied, as was the related fiber tract; Cajal and Dogiel were apparently unaware of this experiment. Essentially the same observation has since been reported by several other investigators (Cowan, Adamson, & Powell, 1961; Huber & Crosby, 1929; Jelgersma, 1896; Kosaka & Hiraiwa, 1915).

Further support for the hypothesis that that cell mass is the origin of the centrifugal fibers to the retina was provided by Wallenberg (1898) using the Marchi method of tracing fiber degeneration. Following lesions of the cell mass, he traced degeneration in the related fiber tract, across the optic chiasma, through the optic nerve, and into the optic nerve layer of the retina. His observation has been repeated with the more refined

silver degeneration techniques (Cowan & Powell, 1962, 1963).

Direct physiological confirmation of the hypothesis was provided by Holden (1966, 1968a). He excited cells in the cell mass afferently and used these orthodromic spikes to block antidromic spikes generated by stimulation of the related fiber tract.

Perlia (1889) had referred to the atrophied cell mass as the nucleus opticus medialis. Craigie (1928) called it the nucleus tractus isthmo-opticus, while Huber and Crosby (1929) used the terms nucleus isthmo-opticus and tractus isthmo-opticus in referring to the cell mass and related fiber tract, respectively. The related terms isthmo-optic nucleus (ION) and isthmo-optic tract (IOT) are commonly used today and will be used here. Except for those and other common terms (i.e., decussation of the fourth nerve, forebrain, lateral geniculate nucleus, optic chiasma, optic nerve, optic tectum, optic tract, posterior commissure, tectal commissure, tecto-isthmal tract), the terminology in this report follows that of Karten and Hodos (1967).

The ION

The brain of the pigeon contains two isthmo-optic nuclei, symmetrically situated about the anterior-posterior axis. The ION is located near the posteromedial border of the optic tectum, along the dorsal boundary of the mesencephalon. The anteroposterior extent of the ION is approximately 0.50 mm; mediolaterally the ION is about 1.00 mm, and dorsoventrally it is about 0.75 mm (Karten & Hodos, 1967). Figure 1a shows the ION, and the structures which

FIGURE 1. DRAWINGS SHOWING THE LOCATION OF THE ION OR IOT AT VARIOUS ANTERIOR LEVELS OF THE PIGEON BRAIN

Drawings were made from transverse sections illustrated by Karten and Hodos (1967) in their stereotaxic atlas; only the left side of the brain is drawn here. The numerical value associated with each section represents the number of millimeters that point is anterior to the zero coordinate. Zero in the atlas is a point located midway between the ears as the head tilts forward 45°.

a. A 1.75

b. A 2.25

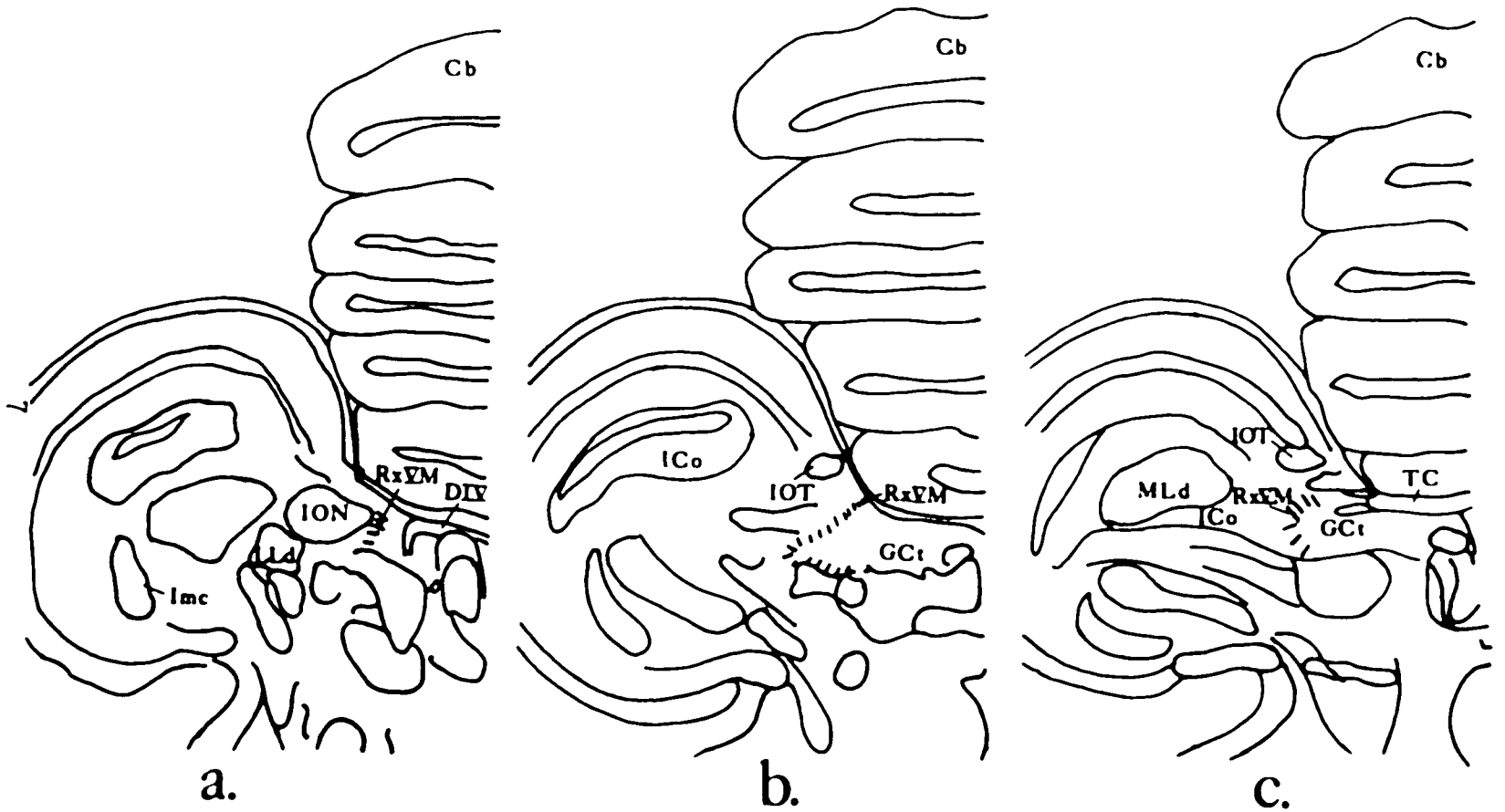
c. A 2.75

d. A 3.25

e. A 3.75

f. A 4.25

See list of abbreviations, Table I.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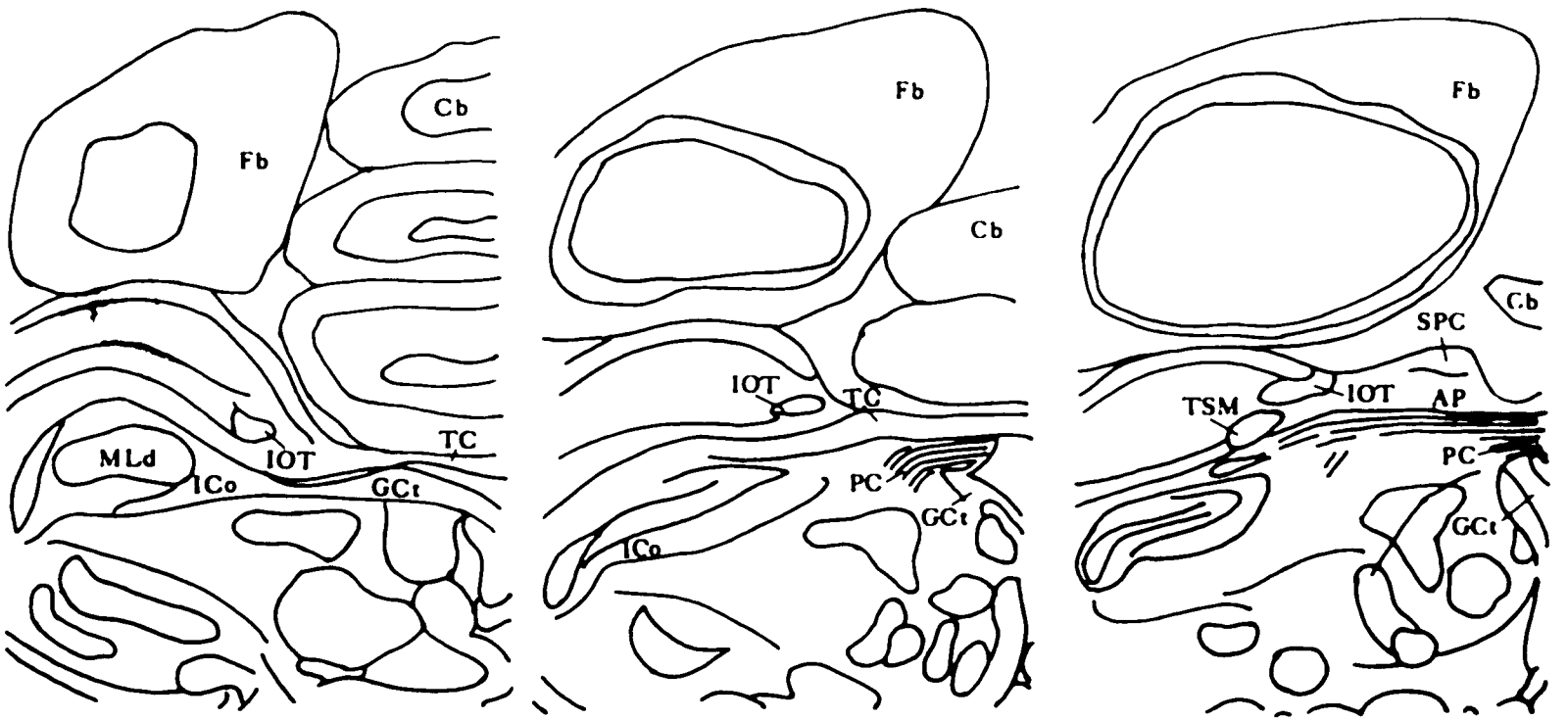
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Cb
SPC
IOT
AP
TSM
PC
GCt
f.

border it, at a point where the ION is the widest both mediolaterally and dorsoventrally. Just posterior to this point, the ION is bordered dorsolaterally by the nucleus isthmi, pars magnocellularis, and dorsomedially by the fibers of the fourth nerve; the fourth nerve fibers also lie very close to the ION just anterior to the point shown in Figure 1a (Karten & Hodos, 1967).

The ION of the pigeon is a highly convoluted lamina of cells arranged in two layers; a narrow layer of dendrites and axons separates the two layers of cell bodies (McGill, Powell, & Cowan, 1966a). The cells of the ION, of which there are approximately 8,000 to 10,000 (Cowan & Powell, 1963; Shortess & Klose, 1975), are typically flask-shaped, each with a single thick dendrite directed toward the center of the ION. The dendrite usually divides into two main branches, each of which gives off several stubby terminals or claw-like branches on which the afferent fibers synapse (Cowan, 1970).

The pigeon ION is folded basically in an S-shape. A major portion of the upper border is bent forward and downward, while the entire lower border is bent backward and upward (McGill et al., 1966a).

The Optic Tectum and its Afferent Retinal Projection

The ION of the pigeon receives its only known afferents from the ipsilateral optic tectum (Cowan & Powell, 1963; McGill, 1964; McGill et al., 1966a; Wallenberg, 1898). The avian optic

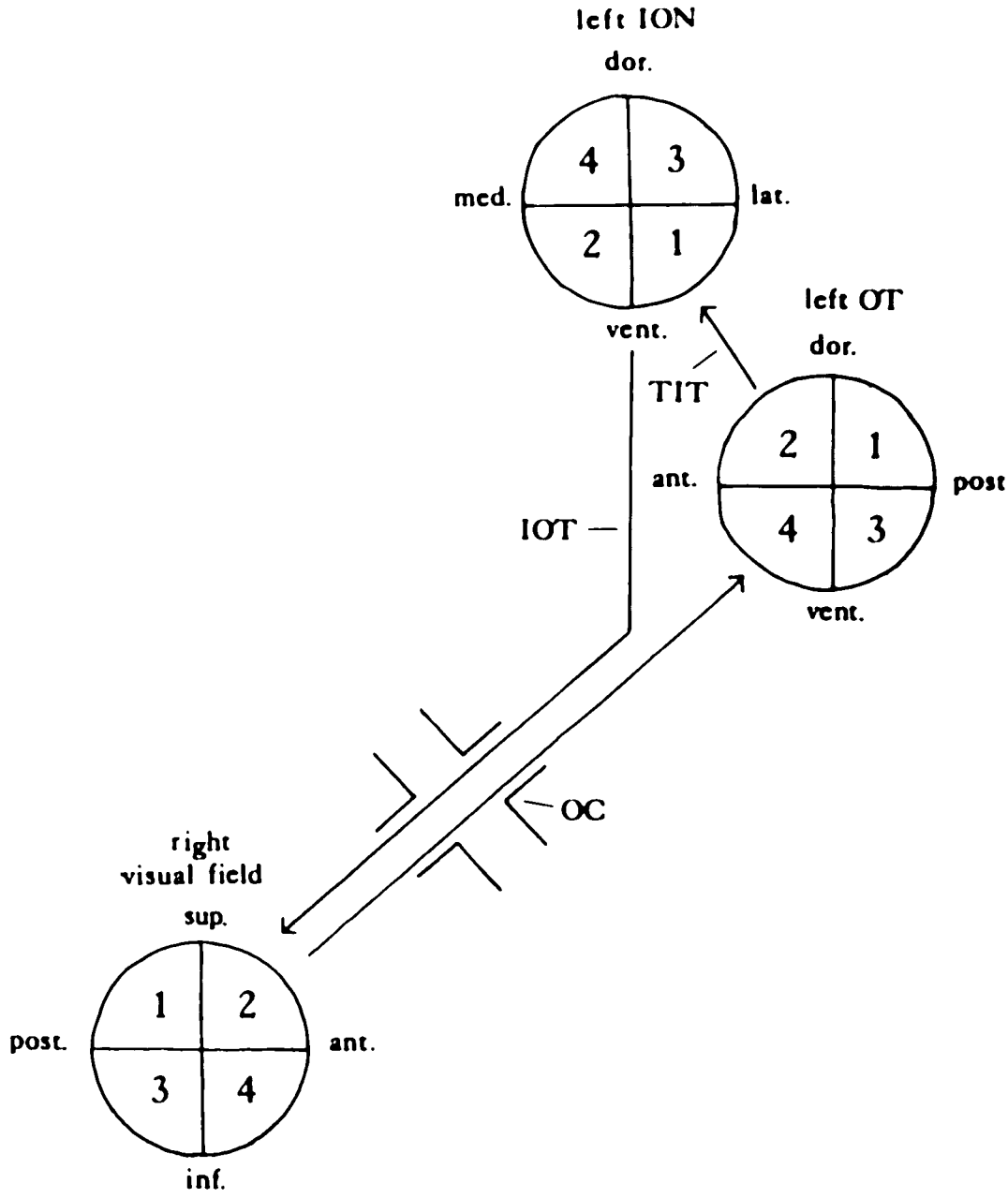
tecta, considered to be the functional analogues of the mammalian superior colliculi, are the primary termination areas of retinal ganglion cells, although there are also retinal projections to a number of thalamic nuclei. Optic nerve fibers in pigeons cross completely at the optic chiasma, and those projecting to the optic tectum form the outer layer of the tectum, the stratum opticum, but terminate in the adjacent deeper layer, the stratum griseum et fibrosum superficiale (Cowan et al., 1961). The pigeon optic tectum actually consists of five primary layers. Adjacent to the stratum griseum et fibrosum superficiale is the stratum griseum centrale, with the deeper layers being the stratum album centrale and substantia grisea et fibrosa periventricularis, in that order (Karten & Hodos, 1967).

The optic tectum of the pigeon is topographically organized with respect to the retina and, thus, the visual field. As can be seen from Figure 2, the upper half of the visual field (i.e., the lower retinal quadrants) is represented on the dorsal portion of the tectum, the lower half of the visual field (i.e., the upper retinal quadrants) on the ventral portion. Further, the posterior half of the visual field (or, nasal retinal quadrants) is represented on the posterior portion of the tectum, the anterior half of the visual field (or, temporal retinal quadrants) on the anterior portion (McGill, 1964; McGill et al., 1966a). This organization is consistent with that found electrophysiologically

FIGURE 2. DRAWINGS SHOWING THE TOPOGRAPHICAL ORGANIZATION OF THE OPTIC TECTUM AND ION WITH RESPECT TO THE VISUAL FIELD

The figure is adapted, in part, from McGill, Powell, and Cowan (1966b). The diagram shows that the upper quadrants of the visual field are represented on the dorsal quadrants of the optic tectum, the anterior quadrants of the visual field on the anterior quadrants of the tectum. The dorsal quadrants of the optic tectum project, in turn, to the ventral quadrants of the ION, the anterior quadrants of the tectum to the medial quadrants of the ION. Finally, the dorsal quadrants of the ION are related to the inferior quadrants of the visual field, the medial quadrants of the ION to the anterior quadrants of the visual field.

See list of abbreviations, Table I.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by Hamdi and Whitteridge (1954) and Tarpley (1976); in both studies the fovea, which is located just slightly ventral and temporal to the center of the eye and serves the lateral visual field, was reported to be represented on the lateral aspect of the tectum. There is another area of high cell density, called the red field, in the upper portion of the temporal retina (Galifret, 1968). This zone would appear to serve the lower portion of the anterior visual field.

The Tectal Projection to the ION

The afferents from the pigeon optic tectum project to the ION via a rather well-defined pathway called the tecto-isthmal tract (TIT) (Cowan & Powell, 1963; McGill et al., 1966a; Wallenberg, 1898). There appears to be a direct connection between the retinal input to the optic tectum and the cells of origin of the TIT, as McGill et al. (1966a) found that superficial lesions of the optic tectum which extended no deeper than the stratum griseum et fibrosum superficiale produced terminal degeneration in the ION. Electrophysiological data also support the existence of a direct connection (Holden, 1968a, 1968b), as well as the existence of a more complex, indirect connection (Holden, 1968b).

The retinotopic organization of the pigeon optic tectum is preserved in the projection of the TIT upon the ION (Figure 2). The dorsal half of the tectum projects to the ventral half of the ION, the anterior half of the tectum to the medial ION. The

retina is, thus, secondarily represented on the ION in such a way that the upper half of the visual field is represented on the ventral portion of the ION, the anterior half of the visual field on the medial portion (McGill, 1964; McGill et al., 1966a). This organization is consistent with that found electrophysiologically by Holden and Powell (1972) who further reported that, while the inferior visual field was represented on the body and "anterior limb" of the pigeon ION, the representation of the superior visual field was confined to the "posterior limb" and thus occupied a much smaller portion of the ION. Holden and Powell (1972) also reported that the representation of the anterior inferior quadrant of the visual field was greater than that of the posterior inferior quadrant, and that of the central portion of the anterior inferior quadrant was greater than that of the peripheral portion. Such a representation of the pigeon's visual field suggests that the ION may have a role in the guidance of pecking, since the tip of the beak lies in the central portion of the anterior inferior quadrant.

The Centrifugal Projection to the Retina

The axons of the ION cells of the pigeon form a fibrous capsule about the ION (Cowan, 1970). These fibers emerge from the ION at the anterior end to form the IOT. For about the next 0.10 mm, the course of the fibers is ventrolateral, after which it becomes dorsal. At a point approximately 0.25 mm anterior to

the ION, the well-defined IOT is located along the medial edge of the optic tectum, very close to the cerebellum (Figure 1b). Lateral to the IOT there is the nucleus intercollicularis (ICo); ventral is the radix mesencephalicus nervi trigemini, bordered medially and ventrally by the substantia grisea centralis (Karten & Hodos, 1967).

Ventrolateral to the IOT, 0.25 mm further anterior, is the nucleus mesencephalicus lateralis, pars dorsalis, separated from the IOT by the ICo. Ventromedial to the IOT, beginning 0.25 mm further forward, lies the tectal commissure (TC) (Figure 1c). The forebrain lies dorsal to the centrifugal pathway beginning about 0.50 mm further anterior (Figure 1d). Forward an additional 0.50 mm, the posterior commissure lies ventromedial to the centrifugal pathway but is separated from it by the TC, which there borders the IOT ventrally and medially (Figure 1e). Approximately 0.25 mm further forward, the nucleus tractus septomesencephalici and the area pretectalis border the IOT medially (Figure 1f) (Karten & Hodos, 1967).

Further anterior the IOT and optic tract join. The centrifugal fibers initially appear as a fairly compact bundle along the medial aspect of the optic tract, although just forward the bundle is more laterally situated in the optic tract. Just posterior to the optic chiasma, most of the centrifugal fibers lie along the dorsal aspect of the optic tract while some are

located at the extreme ventrolateral margin of the tract. Just anterior to the chiasma, the centrifugal fibers are a fairly compact bundle in the medial third of the contralateral optic nerve; further forward the bundle lies at the dorsolateral aspect of the nerve. Just posterior to the optic nerve head, the centrifugal fibers are spread across the entire width of the nerve (Cowan & Powell, 1963).

Centrifugal fiber terminals are distributed across the entire expanse of the pigeon retina (Cajal, 1911; Cowan & Powell, 1963; Dogiel, 1895; Dowling & Cowan, 1966; Maturana & Frenk, 1965). However, Maturana and Frenk (1965) found the centrifugal fiber endings to be evenly distributed across the retina, while Dogiel (1895) and Dowling and Cowan (1966) found the number of endings to be markedly reduced in the periphery.

The ION of the pigeon projects to the retina in such a way that the dorsal half of the ION is related to the inferior half of the visual field, the medial half of the ION to the anterior half of the visual field (McGill, 1964; McGill, Powell, & Cowan, 1966b) (Figure 2). Since the dorsal and medial halves of the ION are related, through the optic tectum, to the inferior and anterior halves of the visual field, respectively, each retinal quadrant is reciprocally connected with that quadrant of the ION from which it receives the centrifugal innervation.

Maturana and Frenk (1965) counted the number of centrifugal

fiber endings in a unit area of pigeon retina and estimated from that figure that the entire retina contains no fewer than 100,000 centrifugal fiber terminals. Although most centrifugal fiber branching occurs in the retina itself, a fair amount appears to take place in the nerve, as Cowan and Powell (1963) found the diameter of the centrifugal fibers to be smaller anterior to the optic chiasma than posterior to it. Cowan (1970) reported that there were about 12,000 fibers in the IOT at a point just rostral to the origin of the IOT. While this could mean that some branching has already occurred, it is also possible that the figure is a more representative or accurate estimate of the number of cells in the pigeon ION.

The ION of the pigeon has been reported to send efferents to structures other than the retina. A few investigators observed centrifugal fibers at the lateral geniculate nucleus but were unable to positively confirm the existence of synaptic contacts there (Cowan & Powell, 1963; Wallenberg, 1898). It is a problem to discriminate the degeneration of preterminals from that of passage fibers. One team of investigators did report the presence of preterminal degeneration in the lateral geniculate nucleus following ION lesions, but only in the diffuse cell area of the dorsal portion (Galifret, Condé-Courtine, Repérant, & Servière, 1971). Galifret et al. (1971) also reported some instances of preterminal degeneration in the area pretectalis

diffusus; the investigators felt that the nucleus ventrolateralis thalami might also contain isthmo-optic preterminals.

Centrifugal Fiber Termination in the Retina

The centrifugal fibers to the pigeon retina have been found to terminate primarily near the junction of the inner nuclear and inner plexiform layers of the retina (Cajal, 1911; Cowan & Powell, 1963; Dogiel, 1895; Dowling & Cowan, 1966; Maturana & Frenk, 1965). Three basic types of centrifugal fiber endings have been described; pericellular nest, basal, and deep. All investigators observed the first type of centrifugal fiber which, after breaking up into several branches, terminated by forming a "pericellular nest" around the soma of an amacrine cell. Maturana and Frenk (1965) also found some centrifugal fiber branches which originated in the nests themselves and terminated on the same nest or on one to three neighboring cells.

Most investigators observed the second type of centrifugal fiber which, after breaking up into several branches which ran along the inner nuclear-inner plexiform boundary, terminated on the basal portion of one or more amacrines (Cajal, 1911; Dogiel, 1895; Dowling & Cowan, 1966; Maturana & Frenk, 1965). Cajal (1911) observed the pericellular nest type ending most frequently, Dowling and Cowan (1966), the basal type ending. The basal type ending had appeared most frequently in an earlier investigation by Cajal (1889) of the finch retina.

Cajal (1911) and Dowling and Cowan (1966) observed the third mode of centrifugal fiber termination, characterized by fibers which ascended to an unspecified ending deep in the amacrine cell layer.

Aside from Cowan and Powell (1963), who observed only the pericellular nest type ending, all investigators agreed that the amacrines cells upon which nests were found were different in appearance from those upon which the basal type endings were found. The investigators did not agree, however, as to the type of amacrine associated with each of the modes of termination; both Cowan (1970) and Rodieck (1973) compared the results of the investigations. Cajal (1911) and Dowling and Cowan (1966) agreed that the amacrines associated with the deep type ending were distinctly different in appearance from those associated with the basal type ending.

Maturana and Frenk (1965) found centrifugal fiber endings on the basal portion of displaced ganglion cells, while Dowling and Cowan (1966) found no centrifugal fiber terminals on those cells.

Morphologically, the IOT of the pigeon appears to be the efferent limb of a feedback loop to the retina. It is conceivable, then, that the centrifugal system of the pigeon functions as a fine tuning mechanism in the service of such behaviors as pecking or visual tracking.

Since the centrifugal fibers have largely been found to

terminate on amacrine cells, a large proportion of which terminate on ganglion cells, many studies on the function of the centrifugal fiber system have focused on the ganglion cells and their response to centrifugal fiber influences.

Receptive Field Properties of Retinal Ganglion Cells

While the role of the amacrine cells in the pigeon retina has yet to be determined, the fact that there are more amacrine-to-ganglion synapses than bipolar-to-ganglion ones (Dubin, 1970; Yazulla, 1974) suggests that the amacrine cells are important. The pigeon retina also contains a large number of amacrine-to-amacrine connections as well as some amacrine-to-bipolar contacts (Dubin, 1970; Yazulla, 1974). The receptive fields of ganglion cells in the pigeon retina (Holden, 1969; Maturana, 1962; Maturana & Frenk, 1963; Pearlman & Hughes, 1976a) have been reported to be more complex than those of vertebrates like the cat (Wiesel, 1960) and the monkey (Hubel & Wiesel, 1960). Since the cat and monkey retinas have lower ratios of amacrine-to-ganglion to bipolar-to-ganglion synapses than the pigeon (Dowling, 1968), amacrine cells may play a more significant functional role in increasing the complexity of ganglion cell receptive fields in the pigeon.

Most ganglion cells described for the pigeon retina were reported to have a central region which responded both to the "on" and the "off" of a small spot of light (Holden, 1969;

Maturana, 1962; Pearlman & Hughes, 1976a). Surrounding the central region of all those cell in Pearlman and Hughes' (1976a) study, and most of those cells in Holden's (1969) study, an inhibitory zone was found. This zone produced no response when illuminated alone but partially or totally suppressed the center response whenever both regions were illuminated at the same time. The surrounds of the remaining ganglion cells in the Holden (1969) study gave "off" responses. Most of the ganglion cells in each of the three investigations responded to moving stimuli. In each study, ganglion cells were found that responded optimally to a stimulus moving in a particular direction and not at all, or very weakly, to a stimulus moving in the opposite, or null, direction. Also described in each study were directionally non-selective cells. Still other variations in retinal ganglion cell responses have been described by Maturana (1962), Maturana and Frenk (1963), and Pearlman and Hughes (1976a).

Centrifugal Effects upon Retinal Ganglion Cells

In attempts to determine the functional role of centrifugal fibers to the avian retina, the responses of retinal ganglion cells to light have been examined after both stimulation and cooling of the centrifugal system. These complementary approaches have yielded essentially the same result: Overall ganglion cell responses were enhanced under centrifugal fiber influence. No ganglion cells responded directly to IOT stimulation. Galifret

et al. (1971) found that the gross optic tract response to a flash of light was enhanced when the pigeon ION was activated by electrical stimulation of the ION or the optic tectum. Ertchenkov, Gusselnikov, and Zaborskis (1972) found that the responses of pigeon retinal ganglion cells to visual stimulation were enhanced when the IOT was electrically stimulated at the same time but the receptive field characteristics were unchanged. While all receptive field types Ertchenkov et al. (1972) tested were affected, cells with weak inhibitory fields were never affected.

Response enhancement upon electrical stimulation of the IOT has been described for ganglion cells in the chicken retina (Miles, 1970, 1972a) which appear to be quite similar to those in the pigeon (Miles, 1972b). Miles (1970, 1972a) found that the effect of IOT stimulation on the ganglion cell response to a small spot of light was slight, while the effect on the response to a large spot of light was fairly dramatic. Large spots of light which normally gave rise to little or no firing because of surround inhibition elicited vigorous firing when stimulus presentation was combined with IOT stimulation. Stimulation of the IOT usually appeared to suppress the inhibitory surround (disinhibition), as responses in most instances were enhanced only when a centered spot of light and annulus of light were presented together in the visual field. Occasionally, IOT

stimulation seemed to facilitate the center response; in these cases, responses were enhanced only during the presentation of the centered spot of light.

Miles (1972) attempted to examine the effects of a reversible cold block of the IOT on ganglion cell responses. Probably for technical reasons, he was usually unable to find any clear cut effects; however, in four cells whose responses to large spots of light were enhanced by the prior passage of a visual stimulus, cooling the IOT abolished the enhancement. In a more successful attempt to eliminate centrifugal effects, Pearlman and Hughes (1976b) examined ganglion cell responses upon cooling the ION of the pigeon. They found that, during cooling, most retinal units produced fewer action potentials to any given stimulus; in addition, the receptive field center of many of the affected ganglion cells decreased in size. Similar to the finding of Ertchenkov et al. (1972) with stimulation, cooling was found to leave basic receptive field properties unaltered. However, contrary to the finding of Ertchenkov et al. (1972), cells with both weak and strong inhibitory surrounds were affected in the same manner, with no direct correlation between strength of surround and magnitude of effect.

The fact that retinal sensitivity appears to be increased under the influence of the centrifugal fiber system is in keeping with the notion that the system acts as a fine tuning device for

visually guided behavior. For example, with pecking, a bird would be able to peck more accurately at an object he could see more clearly.

Receptive Field Properties of ION Cells

The properties of ION cell receptive fields were determined in efforts to identify the circumstances under which the centrifugal fibers might confer their effects upon the retina (Holden, 1970; Holden & Powell, 1972; Miles, 1971, 1972d). Miles (1970) had reported that there was little activity in the chicken ION in the absence of visual stimulation, suggesting that the ION does not have a tonic influence on the retina. The receptive field centers of cells in these studies ranged from 5 to 20° in extent, most being of the on-off type and having purely inhibitory surrounds. Holden and Powell (1972) reported that inhibitory surrounds were wide, each being effective over at least 40 to 50 percent of a pigeon's visual field; ION cells were silent upon uniform illumination of the visual field. Cells in the Holden and Powell (1972) study responded optimally to stimuli 1° or 2° in diameter.

All cells in these investigations responded vigorously to moving targets, often, Holden (1970) reported, at a lower threshold than for stationary targets. Such a property would be expected if the ION has a role in such behaviors as pecking or visual tracking; in the former case, objects in the environment

move across the retina as the head moves backward just prior to the forward movement of the repeated peck. Holden and Powell (1972) found that the preferred velocity of movement among cells in their study was between 5 and 30°/sec, and that most cells showed little habituation. One would not expect ION cells to show much habituation if they are involved in such activities as visual tracking or pecking. Repetitive movements did incur severe habituation in ION cells of the chicken; this effect was both path- and velocity-specific, a change in either aspect usually being able to restore the vigor of firing (Miles, 1971, 1972d).

On the basis of the response to the direction of stimulus movement, Holden and Powell (1972) divided the ION cells into three groups: "directionally non-selective cells," which responded equally to all directions of movement; "posterior minimum cells," which responded to all directions of movement, but unequally, the minimal response being to posteriorly moving stimuli; and, "directionally selective cells," which had distinct preferred and null directions. Holden (1970) had described basically the same three types of cells. In Holden and Powell's (1972) study, most "directionally selective cells" preferred horizontal anterior motion, while the remaining cells of that type preferred either vertical upwards movement or oblique movement in the anterior-upwards or anterior-downwards direction; posterior movement always produced a null response. The response of "posterior minimum cells" is actually a form of directional

selectivity. The general preference among "directionally selective cells" for anterior motion is consistent with a role in pecking, as objects in the environment move forward across the retina as the head is drawn backward prior to the execution of the next peck. "Directionally selective cells" comprised a much smaller proportion of the Holden (1970) and Holden and Powell (1972) cell populations than did cells of the other two types. Each type of ION cell can readily be derived from the convergence of tectal cells described for the pigeon (see Holden, 1969; Tarpley, 1976).

Over half the cells of the chicken ION which Miles (1971, 1972d) examined showed strict directional selectivity (for forward movement), but only at certain target speeds (the 5 to 50°/sec range). Miles (1971, 1972d) also found that advancing dark edges were much more effective than light ones.

In the Holden (1970) and Holden and Powell (1972) studies, the latency of ION cell "on" firing to a 1° spot of light centered in the receptive field was 50 to 65 msec. With such a latency, ION cells, activated by the forward motion of the head, could conceivably sensitize the retina before the execution of the repeated peck. Adding to this latency the 2 to 4 msec it takes an action potential to travel from the ION to optic nerve head (Holden, 1968c), and a few msec for passage across the retina, Holden and Powell (1972) figured that a target moving at 20°/sec across the visual field would have moved only through

1.5° by the time the amacrines could be influenced by the ION. Such timing would be expected if the ION has a role in visual tracking. Intraretinal conduction was estimated at a few msec because the diameter of the centrifugal fibers in the pigeon retina is large (Dowling & Cowan, 1966).

Holden and Powell (1972) found that ION cells responded to radially moving stimuli as well as to tangentially moving ones, producing spikes to movement both toward and away from the eye. Similarly, they found that most ION cells responded to both an increase and a decrease in size of a spot of light centered in the receptive field.

Effects of Lesions of the Centrifugal System on Behavior

To date there have been three behavioral studies of the avian centrifugal system. The first of these, by Rogers and Miles (1972), arose out of the hypothesis of Miles (1972c) that centrifugal fibers act in a dynamic manner to aid in the detection of stimuli that are novel or difficult to discriminate. This "dynamic adaptation" hypothesis represented the integration of Miles' work on the nature of centrifugal effects upon the retina (Miles, 1970, 1972a) with his work on the receptive field properties of ION cells (Miles, 1971, 1972d). According to that hypothesis, the centrifugal system of the normal animal acts to increase the sensitivity of regions of the retina recently thrown into shadow by searching gestures such as lowering the head

toward the ground, thereby increasing the ability of the animal to detect objects of interest there, e.g., insects in undergrowth. If such adaptation does occur, it would seem that one of the main concerns of the centrifugal system is the sensory consequences of an animal's own movements (Miles, 1972c).

Research on the centrifugal components of other systems suggests that centrifugal activity in those systems, too, is intimately related to the sensory side effects of an animal's movements. For example, Russell (1971) found that all voluntary movements of fish and amphibia were accompanied by centrifugal inhibition of the lateral-line organs. Miles (1972c) presented examples of several other systems, and argued that their centrifugal components function to prevent the sensory consequences of an animal's activities from disrupting the monitoring of the external environment. He contended that the centrifugal fibers to the avian retina are concerned with more positive aspects of an animal's movements, such as aiding in the detection of objects of low discriminability. The suggestion that the centrifugal fibers to the avian retina are involved in the visual guidance of pecking is consistent with Miles' contention.

Rogers and Miles (1972) found that "lesioned eyes," i.e., ones contralateral to lesioned isthmo-optic nuclei, responded less readily to a novel stimulus introduced in the posterior

visual field than did "sham-operated eyes." These investigators also found that, while chicks with complete bilateral ION lesions could discriminate seeds from small pebbles almost as well as non-lesioned birds when the objects were in the light areas of a checkerboard shadow pattern, the lesioned birds performed poorly when the objects were in the dark areas. The non-lesioned group included normal, sham-operated birds as well as untreated birds. These results appear to support Miles' (1972c) hypothesis of dynamic adaptation. The failure of birds with ION lesions to notice the novel stimulus may have resulted, however, from the possibility that they were having a difficult time pecking at the grain on which they were feeding at the same time. The fact that lesioned birds performed poorly in the dark areas of the checkerboard shadow pattern may be explained by a guidance difficulty for the more difficult discriminative stimuli.

An additional finding in the checkerboard illumination test was that the pecking rate for the group of birds with ION lesions, either complete or incomplete bilateral, was much lower than that for the group of non-lesioned birds. Such a finding supports the notion that the centrifugal fibers are involved in the guidance of pecking. Rogers and Miles (1972) illustrated the damage for only one lesioned animal, so the extent of involvement of structures other than the ION is unclear for the group of lesioned animals.

In a study primarily designed to examine discrimination performance following lesions of the optic tectum and nuclei isthmi, the isthmo-optic nuclei of three pigeons were lesioned to provide a control for damage to the optic lobe with no damage to the optic tectum (Hodos & Karten, 1974). (Birds with lesions largely confined to the nuclei isthmi had some damage to the tectal strata). Of the "control" birds, one had complete bilateral ION lesions, one had complete damage to one ION and almost complete to the other, and the third had at most 30 percent damage to each. The "control" birds were found to show perfect retention postoperatively for each of four discrimination problems, one intensity and three pattern; all stimuli were suprathreshold in illumination and, thus, not of low discriminability.

In the first of two experiments, Shortess and Klose (1977) found that pigeons with IOT damage had higher $\log_{10}$ latencies of response in a two-choice key pecking task (with suprathreshold stimuli) than did birds with no IOT damage. The effects persisted over the four postoperative days of testing while within each daily session there was a reduction in the $\log_{10}$ latency. This result is consistent with the finding of Rogers and Miles (1972) for pecking rates and, thus, also supports the notion of a visual guidance function. In the second part of their first experiment, Shortess and Klose (1977) found no support for the

idea suggested by Hernández-León (1955) and Bach-y-Rita (1972) that centrifugal fibers in general may function to facilitate the [illegible] of irrelevant and/or repetitive stimuli; this supports the conclusion of Groves and Thompson (1970) that centrifugal fibers are probably not involved in the habituation to unimportant stimuli.

In their second experiment, Shortess and Klose (1977) trained birds with and without IOT damage to discriminate between vertical and horizontal bars, after which time the stimulus key was progressively darkened with neutral density filters. They found that birds with IOT damage had more difficulty discriminating the low luminance targets than did the birds with no IOT damage. This result appears to support Miles' (1972c) hypothesis of dynamic adaptation.

As can be seen from the preceding review, the data are consistent with the notion that the centrifugal system has a role in visual guidance. The present experiment was designed to test this visual guidance hypothesis by comparing the accuracy of pecking a suprathreshold stimulus key for pigeons with and without IOT lesions. It was predicted that those with IOT lesions would be less accurate than those without such lesions.

METHOD

Subjects

Thirteen experimentally naive White Carneaux pigeons (*Columba livia*), obtained from the Palmetto Pigeon Plant, Sumter, South Carolina, were used as subjects. Prior to the experiment, birds were fed a ration containing chlortetracycline for decontamination, as recommended by Arnstein, Cohen, and Meyer (1964). Pigeons were approximately 11 weeks old at the beginning of the experiment. Birds were housed individually and maintained below 85 percent of their free-feeding weights throughout the course of the experiment.

Apparatus

Two different experimental chambers were used as it was believed that pecking styles would be more homogeneous if initial training had taken place in the one chamber, A, since its panel configuration was simpler in certain respects than that of the chamber designed to test the hypothesis, B.

Chamber A was a standard operant conditioning chamber, with an experimental area 49.3 cm x 35.8 cm x 39.8 cm (BRS-Foringer). The chamber was constructed of Formica-covered wood and painted white on the inside. Subjects stood on stainless steel mesh. The front wall of the experimental area was an aluminum panel containing four apertures: three 2.5 cm in

diameter for the response keys, and one 5.7 cm x 4.5 cm for the grain magazine (Model 05610; Ralph Gerbrands Co.). The center of each key aperture was 10.2 cm from the ceiling, and 10.2 cm from the center of the nearest key aperture(s). The middle key aperture was located at the center of the upper portion of the panel, directly above the opening for the grain magazine; the centers of these apertures were 15.2 cm apart.

The projection devices, the response keys, and the grain magazine were located behind the panel. Each stimulus was diffuse white light (111.39 cd/m^2) produced by a one plane digital display unit (Industrial Electronics Engineers, Inc.) which projected the light emitted from a single 28v, 0.7A lamp onto a rear projection screen located 0.7 cm behind the translucent Plexiglas response key. Only the middle and right keys were manipulated by the experimenter. A pigeon seldom, if ever, attempted to operate the left key. A force of 15 g was sufficient to activate an illuminated key. The grain magazine was lit by a 28v, 0.7A lamp during reinforcement.

The experimental area of chamber A was well ventilated, and was illuminated at all times by two 28v, 0.7A lamps mounted behind a strip of white opaque Plexiglas at the top of the panel. A white masking noise of approximately 70 db. re 20 $\mu N/m^2$ was present throughout each session. The chamber was wired to transistor circuitry (BRS/LVE) located in an adjoining room.

Chamber B had an experimental area 30.9 cm x 35.3 cm x 33.9 cm (Lehigh Valley Electronics). The interior and exterior walls of the chamber were made of aluminum, with foam rubber between. The inside of the chamber was painted white. Pigeons stood on stainless steel mesh. The roof of chamber B was modified to include a 14.5 cm x 13.0 cm Plexiglas window at the front of the experimental space, over the area where pigeons stood as they pecked for reinforcement. Over the window was mounted a black-and-white video camera (Model AVC3200; Sony) connected to a half-inch videotape recorder (Model 3600; Sony).

The front wall of the experimental area was a two key aluminum panel (Model 141-12; Lehigh Valley Electronics) modified as shown in Figure 3. Surrounding the key which activated the grain magazine, i.e., the "reinforcement" key (K in Figure 3), was a "surround" key of black Plexiglas which recorded misplaced pecks. A strip of aluminum (P in Figure 3) concealed the surround key mechanism.

The projection device, the reinforcement key, the grain magazine and the noise generator were located behind the panel. The stimulus was diffuse white light (71.95 cd/m^2) produced by a one plane digital display unit which projected the light emitted from a 28v, 0.7A lamp onto the opaque strip of Plexiglas which functioned as the reinforcement key. The luminance of the surround key was approximately 11.99 cd/m^2. The force required

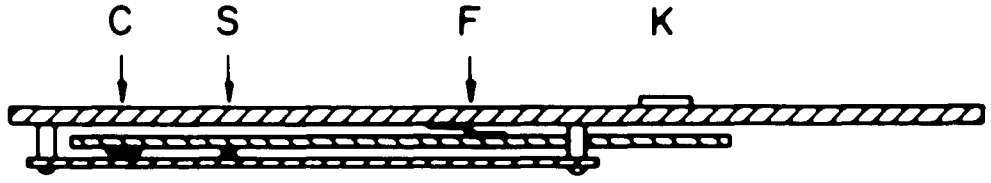
FIGURE 3. DRAWINGS OF THE SURROUND KEY

A two (reinforcement) key panel was modified to include one reinforcement key and a "surround key," i.e., a device which recorded pecks made around the perimeter of the reinforcement key.

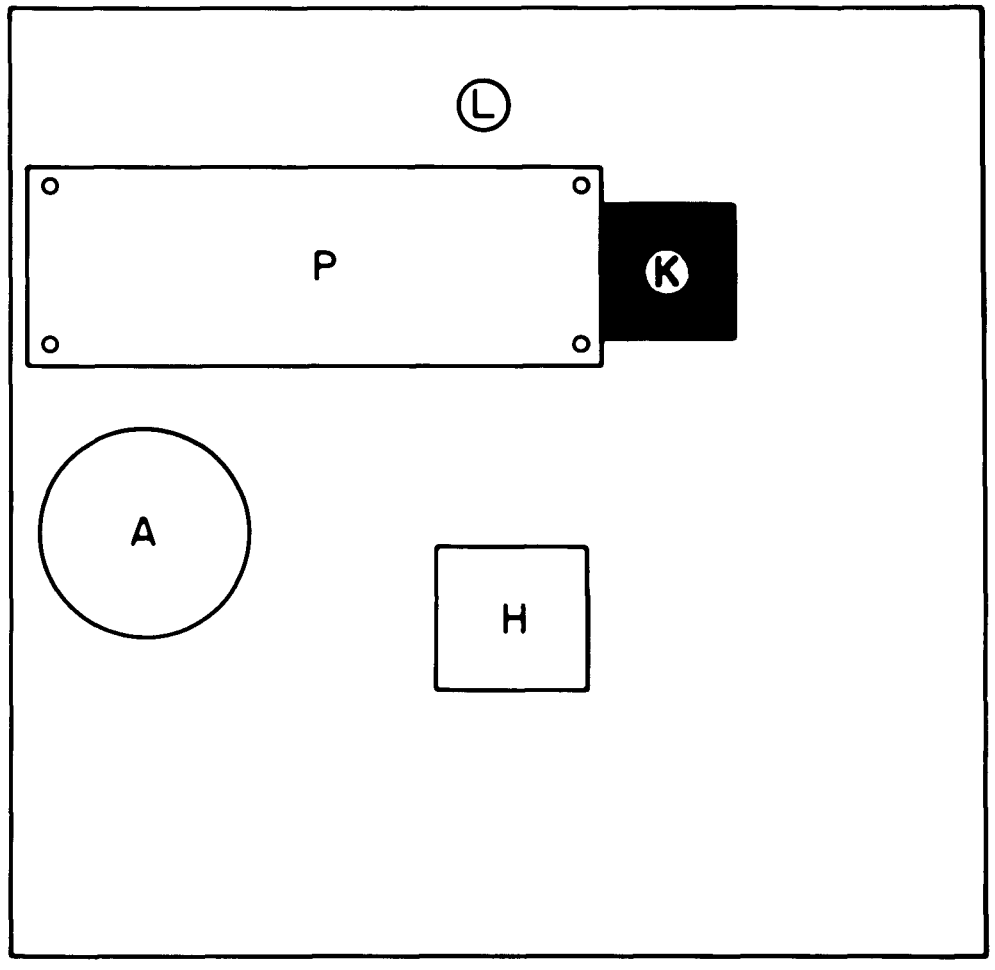
a. This is a drawing of the surround key mechanism, as viewed from above.

b. This is a drawing of the entire front wall of the experimental area of chamber B, as viewed from inside the experimental area; the surround key is represented by the darkened area.

A: speaker for the noise generator; C: contact; F: fulcrum; H: opening to the grain magazine; K: reinforcement key; L: house light; P:coverpiece for the surround key mechanism; S: spring



a.



b.

to activate the reinforcement key was approximately 11 g, that required for the center key was approximately 7 g. The grain magazine was lit by a 28v, 0.7A lamp during reinforcement. A white masking noise of approximately 75 dB re 20 $\mu N/m^2$ was present throughout each session in chamber B.

The experimental area of chamber B was well ventilated. A flourescent lamp (F8T5; Sylvania) mounted behind a strip of white translucent plastic at the upper edge of the rear wall, as well as a 28v, 0.7A lamp located at the center of the panel above the aluminum coverpiece (L in Figure 3), illuminated the experimental area at all times. The transistor circuitry (BRS/LVE) to which the chamber was wired was located in another section of the room.

Procedure

Chamber A was used for the first six days of training. On Day 1, pigeons were trained to eat from the grain magazine after which they were trained to peck at the center key for access to food, by reinforcement of successive approximations. The grain magazine was in the raised position when animals were placed in the chamber on Day 1. The center key only was illuminated, except during reinforcement when it was dark for three sec. Sessions on Day 1 terminated after 100 reinforcements; each bird obtained at least 40 reinforcements automatically.

Except on the days of surgery and recovery, birds had one session per day, seven days per week. Sessions on Days 2 and 3

differed from those on Day 1 only in that the grain magazine was in the lowered position when animals were placed in the chamber. On Days 4, 5, and 6, the right rather than the center key was illuminated, except during reinforcement when the right key was dark for three sec. The grain magazine was in the lowered position when pigeons were placed in the chamber. Sessions on those and all following days terminated after 101 reinforcements.

The remainder of the experimental sessions took place in chamber B. The grain magazine was always in the raised position when birds were placed in the chamber; this constituted the first reinforcement of a session. All reinforcements following the first in a session lasted 2.6 sec.

Birds had four sessions in chamber B before a correction procedure was introduced in order to reduce surround key pecking rates. On Day 11, animals could not obtain reinforcement during the two sec following the first surround key peck on any trial. The first peck which activated the reinforcement key after that delay period gave birds access to food. On Day 12, there was a two sec delay after each surround key peck made before the grain magazine was activated as an attempt to reduce surround key pecking rates further. However, it was not until Day 13, when the reinforcement key became dark during the delay period following each surround key peck, that substantial reductions in surround key pecking rates were effected.

If an animal made no more than 25 surround key pecks during each of four consecutive sessions after Day 12, he was videotaped during his next session. During a videotaped session, there was no correction procedure for surround key pecks. If an animal made less than 26 surround key pecks during that videotaped session, his next session was videotaped. If a pigeon made less than 26 surround key pecks during that session, surgery was performed on the following day. If the number of surround key pecks exceeded 25 during a preoperative videotaped session, the correction procedure of Day 13 was reintroduced the following day. Four consecutive sessions with less than 26 surround key pecks had to occur again before a session was videotaped. Measures taken during an animal's two consecutive videotaped sessions with less than 26 surround key pecks constituted the preoperative data for the animal.

Birds were randomly assigned to treatment groups, eight to the experimental and five to the control. Lesions were attempted in the isthmo-optic tracts in experimentals or in the area just dorsal to each isthmo-optic tract in controls. Both placements usually involve damage to the cerebellum and optic tecta. The experimenter doing the behavioral assessment was blind to this treatment. An animal was not run on the day following surgery but was deprived of food on noon of that day. Postoperative data for an animal were collected on the next two days; sessions on

those days were also videotaped. Pigeons were sacrificed two weeks or more after surgery and their brains examined histologically for damage.

Surgery

Birds were anesthetized with a combination of ketamine hydrochloride (150 mg/kg) and Equi-Thesin (1.50 mg/kg) in dosages reduced by percentage reduction in free-feeding weight (Karten & Hodos, 1967); the dosage of Equi-Thesin was further reduced by 25 percent. Additional injections of ketamine hydrochloride (0.10-0.20 ml) and/or Equi-Thesin (0.02-0.05 ml) were administered as required. All those injections were given in the pectoral muscle.

The anesthetized animal was placed in a Kopf stereotaxic instrument (Model 1204) equipped with a Kopf beakholder. Feathers were clipped and an incision made through the scalp from the region of the forebrain to the insertion of the neck musculature. The skin was retracted and the periosteal connective tissue cleared away with a blunt edge. The bone was then removed over the area of the lesions--the upper layers of bone with a dental drill, the lower ones with fine-tipped forceps. The dura was incised with a corneal knife.

Lesions were placed with a radio-frequency lesion generator (Model RFG-4; Radionics, Inc.). The active electrode was a commercial electrode with a thermistor at the tip. During

lesion-making, the average temperature at the thermistor ranged from 60.25 to 60.75° C. The current delivered at the lesion temperature ranged from 22 to 45 mA; the voltage drop ranged from 14v to greater than 30v. The indifferent electrode was attached to the retractor at the incision.

Lesions were located according to the coordinate system of Karten and Hodos (1967), with the medial-lateral and dorsal-ventral coordinates adjusted for body weight. The greater the free-feeding weight, the more medial and ventral a lesion was placed; at most an adjustment of 0.10 mm was made. Zero in Karten and Hodos' (1967) atlas is a point located midway between the ears as the head tilts forward 45°. The range of coordinates of experimental lesions in the present study were:

7.40 to 7.50 mm dorsal-ventral

2.10 to 2.15 mm medial-lateral

3.00 mm anterior-posterior

The range of coordinates of control lesions were:

8.75 to 9.10 mm dorsal-ventral

2.10 to 2.15 mm medial-lateral

3.00 mm anterior-posterior

After lesioning, the holes were sealed with Cranioplastic Cement (Plastic Products Co.) and the scalp sutured. Birds were given 0.33 ml Crysticillin (procaine penicillin G) in the thigh muscles and, after partial recovery, returned to their

home cages.

Histology

Birds were anesthetized with lethal dosages of Equi-Thesin (0.35-0.45 ml) and each perfused via the left ventricle with 180 ml of physiological saline, followed by 180 ml of 10 percent formalin. Animals were immediately decapitated and, after skin and beak were removed, heads were immersed in 10 percent formalin. Within 12 hours the eyes and all muscle tissue were removed, after which the skulls were placed back in the formalin where they were allowed to harden for at least seven days. Brains were then dissected from the skulls and immersed in 50 ml of 10 percent formalin to which 5 g of granulated sugar had been added. Brains soaked in that mixture for a minimum of 24 hours.

Brains were blocked at a rostral to caudal cut at an angle 80° to the horizontal plane established by the dorsal surface of the forebrain and cerebellum (Karten & Hodos, 1967). Blocked brains were embedded in Tissue-Tek O.C.T. Compound (Ames) and placed in a microtome-cryostat (Model CTD; International Equipment Co.) set at -18° C for 20 minutes, after which they were sliced into transverse sections 40 μm thick. Sections were placed serially in ice cube trays filled with distilled water. After being dipped in a mixture of 250 ml distilled water and 25 drops Mayers Adhesive Albumen (Carolina Biological Supply Co.), sections were mounted alternately on slide to provide two series. Sections

were dried for approximately 13 hours on a slide warmer (Model 12-594-5V3; Fisher Scientific) set at 45° C. One series was then stained with a Nissl material stain, the other with a myelin stain (both from Skinner, 1971).

Lesion damage was evaluated independently by the experimenter and one other person, both of whom were blind to treatment of particular animals. Any small differences in evaluation were resolved by reexamination and discussion.

Data Analysis

A 12 channel serial/parallel entry print-out counter (Model POC-112; BRS/LVE) provided records of surround key pecks from termination of reinforcement to termination of reinforcement. For each of the thirteen birds, the number of surround key pecks made during the bird's two preoperative sessions was subtracted from the number made during his two postoperative sessions and the difference ranked along with his total IOT damage; the Spearman rank correlation coefficient, r_s, (Siegel, 1956) was computed for those data. That coefficient was also computed for the ranking of total IOT damage with difference scores for the 13 birds for the number of trials with surround key pecks.

The Mann Whitney U (Siegel, 1956) was computed for each of the two sets of difference scores; for that test, the experimental group included all birds with IOT or ION damage, while the control group included those with no IOT or ION damage.

The videotapes of the two preoperative and two postoperative sessions were scored for total pecks, which included those pecks too short to activate either the reinforcement or surround key as well as those which did activate either key. The entire group of pecks was called "video" pecks. The experimenter was blind to treatment of particular animals while scoring the videotapes. The Mann Whitney U and Spearman r_s were computed for difference scores for both the number of video pecks per session and the number of trials with video pecks per session. The 100 pecks per session which activated the reinforcement key were excluded from those analyses for ease of calculation.

The amount of time from termination of one reinforcement to onset of the next was recorded for each trial in 0.2 sec units by the print-out counter. An unweighted means analysis of variance (Winer, 1962) for four factors was performed on the data for the second preoperative and first postoperative days: A(Groups of subjects) x B(Blocks of 20 trials within days) x C(Days) x D(Subjects). Blocks and Days were repeated measures. Each cell entry in the AxBxCxD table is the mean of the $\log_{10}$ latencies for the appropriate block of 20 trials.

All pre- and postoperative data are presented in the Appendices.

RESULTS

Histology

Figure 4 characterizes the lesions for all birds. While every bird in which experimental lesions were attempted had some IOT damage, complete bilateral IOT damage was definitely established for only one bird (12-45). Bird 12-27 may have had complete bilateral IOT damage; it is unclear whether or not a small part of one IOT, at most five percent, remained intact. Although control birds had damage to only the cerebellum and the optic tectum, experimental birds typically had damage to a number of structures in addition to the IOT, cerebellum, and optic tectum. Table II summarizes the damage for each bird.

Behavior

No bird showed any obvious general motor or oculomotor deficits during the postoperative sessions. Also, all birds responded postoperatively with normal pupillary reactions to light level changes.

There is a significant positive correlation between total amount of IOT damage for each of the 13 birds and the difference scores for number of surround key pecks, $r_s = 0.58$, $N = 13$, $p < 0.05$, as well as between total IOT damage and the difference scores for number of trials with surround key pecks, $r_s = 0.65$, $N = 13$, $p < 0.05$. No correlation involving video pecks is

FIGURE 4. DRAWINGS SHOWING LESION DAMAGE FOR EACH BIRD

Lesion damage for each animal is shown in heavy black on a section representing an anterior level at or near the point of maximum lesion.

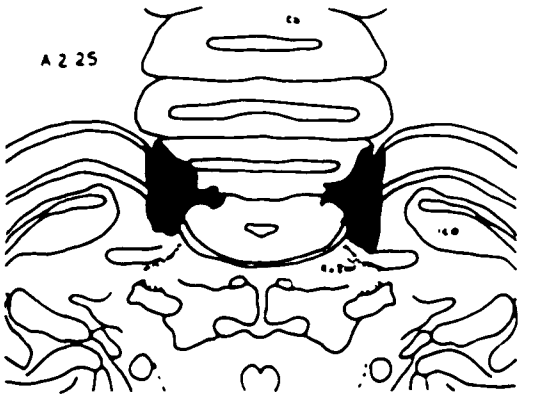
Experimentals: 12-45, 12-27, 12-36, 12-29, 12-31, 12-47, 12-37, 12-48;

Controls: 12-42, 12-46, 12-30, 12-40, 12-44

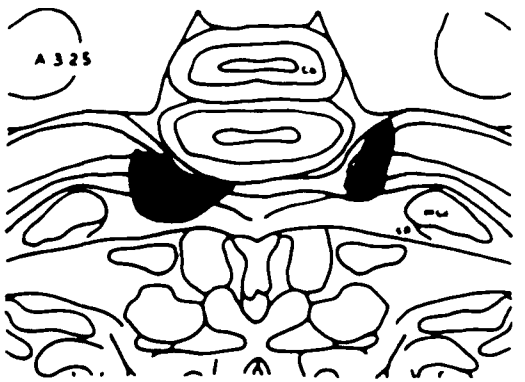
Cb: cerebellum; ICo: nucleus intercollicularis; MLd: nucleus mesencephalicus lateralis, pars dorsalis; RxV̲M: radix mesencephalicus nervi trigemini; TIO: isthmo-optic tract

12-45

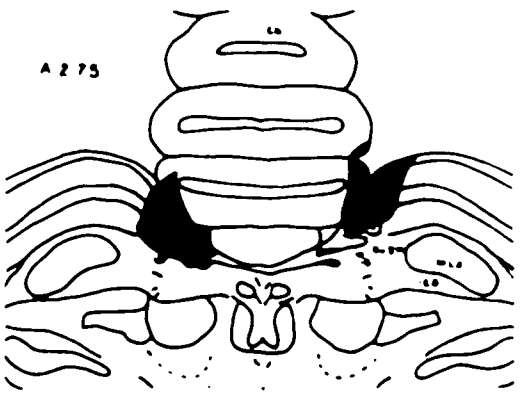
12-27



12-36

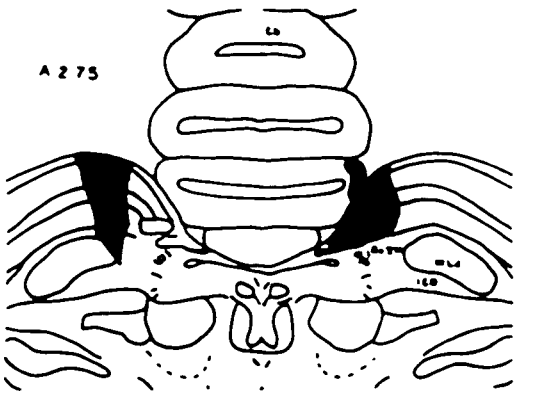


12-29

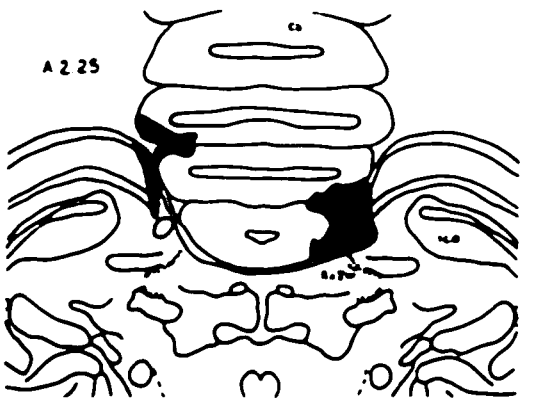


12-31

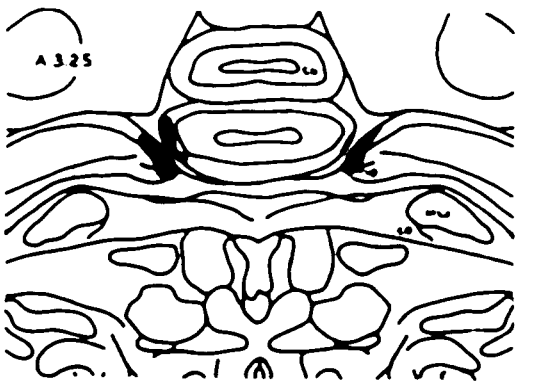
12-47



12-37



12-48



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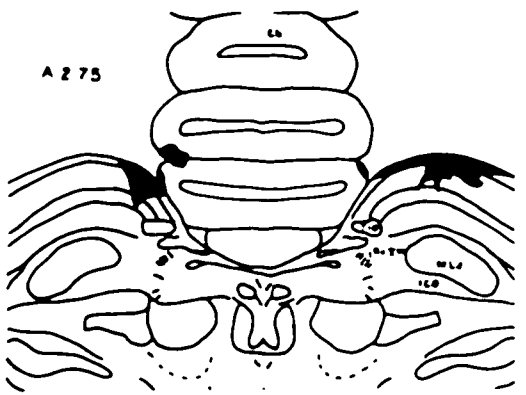

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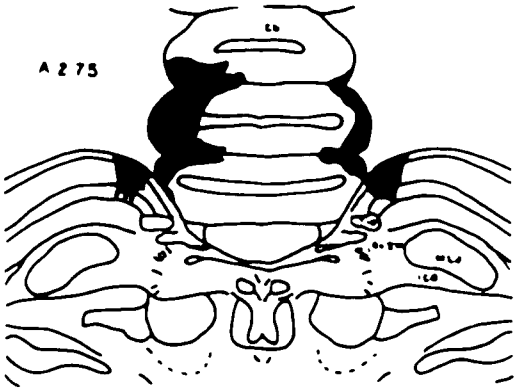

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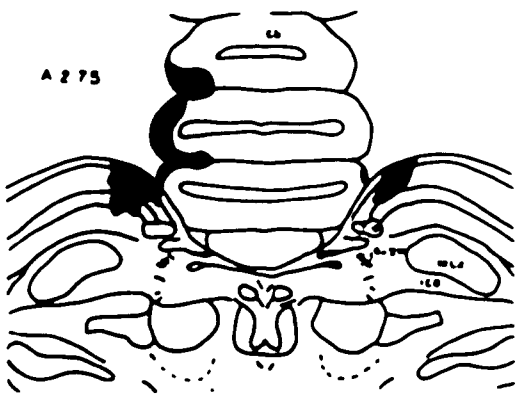
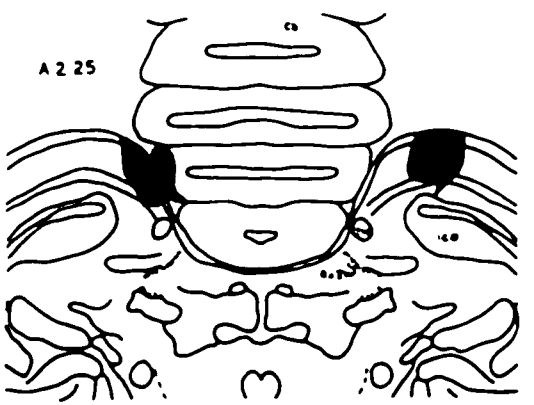


12-40



12-44

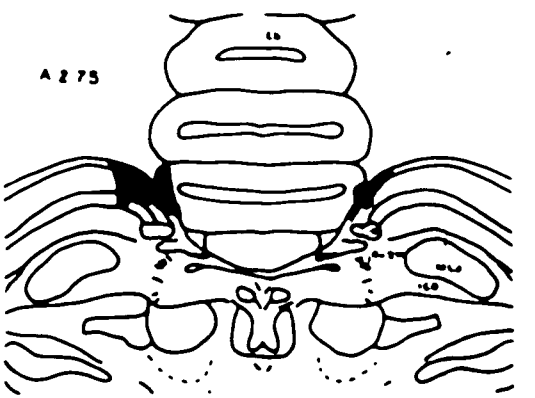


TABLE II. LESION DAMAGE

	IOT		Cb		GCt		RxVM		ICo		Imc		DIV	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R
12-45	100	100	1	0	2	1	2	0	0	2	1	0	1	0
12-27	95-100	100	2	2	0	1	0	0	0	1	0	0	0	0
12-36	100	95	0	0	2	1	2	0	2	1	0	0	0	0
12-29	100	60-70	1	1	2	0	2	0	1	0	0	0	1	0
12-31	20-30	100	1	1	0	0	0	0	0	0	0	0	0	0
12-47	0	100	0	1	0	1	0	0	1	1	0	0	0	0
12-37	0	100	1	1	0	1	0	2	0	0	0	0	0	1
12-48	10-20	10-15	1	1	0	0	0	0	0	0	0	0	0	0
12-42	0	0	1	1	0	0	0	0	0	0	0	0	0	0
12-46	0	0	2	1	0	0	0	0	0	0	0	0	0	0
12-30	0	0	2	1	0	0	0	0	0	0	0	0	0	0
12-40	0	0	1	0	0	0	0	0	0	0	0	0	0	0
12-44	0	0	1	1	0	0	0	0	0	0	0	0	0	0

0: no damage
1: slight (<10%) damage
2: moderate (10-50%) damage
?: possible damage

L: left side of the brain
R: right side of the brain

Isthmo-optic tract damage represented by actual percent

TABLE II. (CONT'D)

	LLd		MLd		TC		PC		TSM		AP		SPC		Pb	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
12-45	2	0	1	0	2	2	0	1	0	2	0	1	0	0	0	0
12-27	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
12-36	0	0	2	1	2	0	2	0	0	0	1	0	2	0	?	?
12-29	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
12-31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
12-47	0	0	1	0	0	2	0	0	0	0	0	0	0	0	?	0
12-37	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
12-48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12-46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?
12-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
12-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
12-44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

0: no damage
1: slight (<10%) damage
2: moderate (10-50%) damage
?: possible damage

L: left side of the brain
R: right side of the brain

Isthmo-optic tract damage represented by actual percent

statistically significant ($p > 0.05$).

The difference between the experimental and control groups on the difference scores for number of trials with surround key pecks is marginally significant, Mann Whitney $U = 8.5$, $n_1 = 5$, $n_2 = 8$, $p < 0.06$, with the experimental group having made more surround key pecks postoperatively as compared with preoperatively than did the control group.

Analysis of the latency data shows that there is a significant main effect of blocks of trials, $F(4,44) = 4.64$, $p < 0.01$, and days, $F(1,11) = 10.83$, $p < 0.01$. Mean $\log_{10}$ latencies were higher postoperatively than preoperatively; by far the greatest postoperative $\log_{10}$ latency elevation was for the first block of 20 trials, an effect which helped to produce a significant Blocks x Days interaction, $F(4,44) = 2.73$, $p < 0.05$. No F ratios involving groups are statistically significant ($p > 0.05$).

DISCUSSION

While a significant visual guidance deficit did result from the lesions, it is not clear that it was due to IOT damage. Most birds with IOT lesions had damage to several structures not damaged in controls, with the total amount of IOT damage being correlated with the number of structures involved. The absence in the present study of more birds with complete bilateral lesions also limits any conclusions. Thus, the question as to whether the centrifugal system has a role in this visual guidance task is essentially unanswered, although results with surround key pecks are consistent with such a role.

The lack, in this study, of any significant result involving video pecks gains some clarity upon close examination of the data. Surround key peck measures for a preoperative session were, for most birds, almost always considerably less than the respective measures for video pecks. Since the video peck measures were for two kinds of pecking—the kind which activated the surround key, as well as the kind which was too short to activate any key—it appears that with the normal animal short pecks fairly often precede the peck which finally activates the grain magazine. Any short pecking caused by experimental lesions, then, would have had to be even more numerous or frequent to reach statistical significance. Of course, it is also possible that experimental

lesions only caused pecks to be misplaced in the plane of the surround key. This might well be the case if the present key pecking task actually involved two mechanisms: (1) a short preparatory peck; and, (2) the actual guidance mechanism.

The finding in the latency data of no significant difference between groups fails to replicate such effects reported by Rogers and Miles (1972) and Shortess and Klose (1977). That suggests that there may be a task-specific aspect to those effects. It is possible that birds in the present study relied much less on vision than in either of the other studies. Rogers and Miles' (1972) task involved the discrimination of seeds from small pebbles. The motor pattern involved in getting from grain magazine to reinforcement key could be more firmly established on the basis of kinesthetic cues in the present single reinforcement key task than in Shortess and Klose's (1977) two reinforcement key task.

It would appear that any future attempt to test whether the centrifugal system has a role in visual guidance might employ the surround key approach, since a marginally significant difference between groups was obtained with a relatively small group of subjects. It is imperative that, in any future attempt, experimental and control groups be better matched in terms of the structures damaged. It is, however, very difficult to confine lesions to the IOT, or to produce entirely adequate controls. One may want to design the experimental group to include only

smaller, partial IOT lesions so that any significant effect would have greater interpretability. The configuration of experimental lesions in the present study, however, does suggest that a somewhat more ventral placement in combination with a considerable reduction in lesion temperature might produce complete bilateral IOT lesions with little surrounding structure damage. It is possible that under that circumstance the difference in visually guided performance between groups would be great. On the other hand if it were not, the role of the surround key structure in visual guidance should be evaluated. Perhaps the use of a match-to-sample task wherein each match key is encircled by a surround key would cause responses to be more dependent on visual cues, particularly if the match had to be made within a limited amount of time.

The suggestion that the centrifugal fibers to the avian retina have a role in visual guidance seems a reasonable one given what is known about the fibers in the pigeon. The extent of the representation on the ION of the region of the visual field in which the tip of the beak resides is particularly supportive of the suggestion. The fact that objects move forward across the retina as the head is drawn backward just prior to the execution of a peck coincides with the vigorous response of ION units to moving targets and the general preference among directionally selective units for anteriorly moving targets. In fact, if there

is a preparatory mechanism as was suggested above, its function may be in whole or in part to insure the activation of ION units as would occur between the forward movements of the preparatory and actual pecks. The apparent increase in retinal sensitivity upon activation of the centrifugal system may have the purpose of increasing pecking accuracy. If this is the case, Miles' (1972c) notion that the centrifugal fibers to the avian retina are concerned with the positive aspects of an animal's movements would be supported. It may be, however, that the increase in retinal sensitivity functions to compensate for the reduction in illumination that objects often undergo due to the position of the head while pecking; centrifugal activity would still have the effect of increasing pecking accuracy. This latter possibility is in keeping with the results of Rogers and Miles (1972) and Shortess and Klose (1977) with low luminance targets.

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APPENDIX A: NUMBER OF SURROUND KEY PECKS FOR EACH BIRD FOR BOTH PREOPERATIVE AND BOTH POSTOPERATIVE SESSIONS

	Preop Session 1	Preop Session 2	Postop Session 1	Postop Session 2
12-45	2	4	6	27
12-27	24	8	19	34
12-36	3	4	4	2
12-29	11	2	8	7
12-31	2	4	0	6
12-47	6	0	0	0
12-37	5	5	4	3
12-48	15	13	16	20
12-42	11	16	3	4
12-46	2	0	0	1
12-30	15	0	5	2
12-40	3	3	1	1
12-44	4	18	10	31

APPENDIX B. NUMBER OF TRIALS WITH SURROUND KEY PECKS FOR EACH BIRD FOR BOTH PREOPERATIVE AND BOTH POSTOPERATIVE SESSIONS

	Preop Session 1	Preop Session 2	Postop Session 1	Postop Session 2
12-45	2	4	6	20
12-27	18	7	16	28
12-36	3	3	4	2
12-29	9	2	8	6
12-31	2	4	0	6
12-47	3	0	0	0
12-37	5	5	3	3
12-48	9	9	8	12
12-42	11	14	3	3
12-46	2	0	0	1
12-30	10	0	1	1
12-40	3	3	1	1
12-44	4	9	9	13

APPENDIX C. NUMBER OF VIDEO PECKS MINUS 100 FOR EACH BIRD FOR BOTH PREOPERATIVE AND BOTH POSTOPERATIVE SESSIONS

	Preop Session 1	Preop Session 2	Postop Session 1	Postop Session 2
12-45	43	101	169	133
12-27	30	12	18	32
12-36	11	8	21	22
12-29	37	51	25	40
12-31	32	28	15	58
12-47	22	5	0	2
12-37	26	30	49	23
12-48	34	26	31	23
12-42	12	9	7	18
12-46	46	4	32	12
12-30	21	4	17	7
12-40	17	25	11	9
12-44	12	17	42	44

APPENDIX D. NUMBER OF TRIALS WITH VIDEO PECKS OTHER THAN THOSE WHICH ACTIVATED THE REINFORCEMENT KEY FOR EACH BIRD FOR BOTH PREOPERATIVE AND BOTH POSTOPERATIVE SESSIONS

	Preop Session 1	Preop Session 2	Postop Session 1	Postop Session 2
12-45	27	59	92	80
12-27	19	8	13	28
12-36	11	8	17	15
12-29	30	38	21	27
12-31	23	21	14	34
12-47	17	5	0	2
12-37	22	29	40	22
12-48	17	16	14	20
12-42	11	8	7	17
12-46	30	4	32	12
12-30	13	4	9	5
12-40	13	22	10	9
12-44	11	13	25	23

APPENDIX E. MEAN LOG_{10} LATENCIES OF RESPONSE FOR BLOCKS OF 20 TRIALS FOR BOTH PREOPERATIVE AND BOTH POSTOPERATIVE SESSIONS

Preoperative Session 1

	1-20	21-40	41-60	61-80	81-100
12-45	.80	.76	.80	.87	.87
12-27	.77	.69	.70	.78	.74
12-36	.45	.58	.56	.51	.49
12-29	.56	.31	.43	.39	.43
12-31	.61	.64	.56	.52	.61
12-47	.55	.59	.70	.61	.63
12-37	.52	.37	.46	.44	.45
12-48	.64	.31	.53	.52	.43
12-42	.26	.15	.21	.37	.56
12-46	.52	.66	.76	.53	.47
12-30	.49	.57	.70	.61	.68
12-40	.56	.44	.47	.57	.60
12-44	.57	.44	.51	.53	.53

Preoperative Session 2*

	1-20	21-40	41-60	61-80	81-100
12-45	.83	.93	.91	.78	.86
12-27	.76	.71	.65	.72	.75
12-36	.51	.55	.57	.55	.55
12-29	.35	.34	.26	.25	.40
12-31	.60	.55	.56	.69	.70
12-47	.58	.57	.52	.50	.60
12-37	.64	.48	.54	.44	.43
12-48	.64	.48	.43	.35	.33
12-42	.36	.24	.26	.43	.54
12-46	.57	.52	.52	.46	.51
12-30	.52	.53	.53	.58	.61
12-40	.56	.54	.54	.55	.65
12-44	.61	.57	.54	.61	.53

*This data used in the analysis of variance

Postoperative Session 1*

	1-20	21-40	41-60	61-80	81-100
12-45	1.06	.87	.90	.85	.83
12-27	.68	.68	.65	.67	.73
12-36	.75	.71	.68	.67	.71
12-29	.57	.45	.47	.61	.48
12-31	.67	.62	.59	.64	.58
12-47	.64	.62	.57	.58	.57
12-37	.60	.32	.32	.42	.46
12-48	.75	.52	.46	.42	.46
12-42	.56	.37	.42	.47	.44
12-46	.73	.68	.69	.66	.65
12-30	.59	.58	.63	.70	.65
12-40	.62	.60	.56	.67	.75
12-44	.89	.57	.66	.63	.57

*This data used in the analysis of variance

Postoperative Session 2

	1-20	21-40	41-60	61-80	81-100
12-45	.80	.79	.79	.85	.86
12-27	.75	.54	.68	.62	.74
12-36	.77	.69	.71	.67	.64
12-29	.50	.46	.34	.41	.48
12-31	.80	.70	.80	.69	.83
12-47	.62	.55	.51	.48	.58
12-37	.40	.24	.32	.30	.35
12-48	.56	.50	.24	.40	.30
12-42	.34	.27	.30	.62	.58
12-46	.63	.58	.58	.57	.57
12-30	.55	.52	.55	.74	.57
12-40	.48	.50	.57	.61	.57
12-44	.72	.56	.74	.68	.66

VITA

Monica L. Seech, daughter of Margaret M. Leech, was born on June 23, 1949, in Pittsburgh, Pennsylvania.

Ms. Seech has a Bachelor of Arts degree from Indiana University of Pennsylvania where she graduated with high honors in June, 1971.

The author entered the graduate program at Lehigh University in September, 1972,as a National Science Foundation Trainee. The following academic year Ms. Seech was a C. Kemble Baldwin Fellow, and the following a Research Assistant. During the summer of 1975 she was employed as a Research Assistant at Beaver College, and since then has been working as a Research Scientist at the Center for Social Research at Lehigh.